

THE LIFE HISTORIES OF THE *AUTODICE* AND *STERODICE*  
SPECIES-GROUPS OF *TATOCHILA*  
(LEPIDOPTERA: PIERIDAE)

Arthur M. Shapiro

*Abstract.*—The egg, larva, pupa and host relations of *Tatochila autodice*, *blanchardii*, *sterodice macrodice*, *sterodice sterodice*, *vanvolxemii* and *mercedis* are described. These species occur in temperate to subantarctic Argentina and Chile. The *sterodice* species-group is very homogeneous and seems to be closely related to *T. xanthodice* from Colombia. The *autodice* group shows many divergences in the larva and pupa and is convergent in various characters with a number of Holarctic taxa. *T. mercedis* is somewhat intermediate to the *autodice* group in certain characters.

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This is the third in a series of papers describing the preparatory stages of the Pierini of the Andean region. This tribe has undergone an extraordinary adaptive radiation, with eight endemic genera and about 40 species in non-tropical habitats, from northeastern Colombia to Tierra del Fuego.

The biology of the genus *Tatochila*, *sens. lat.*, was reviewed by Giacomelli (1915) and Jörgensen (1916). The former prepared a hypothetical phylogenetic "tree" based on adult characters, mostly superficial. At that time the early stages of only one species, *T. autodice* (Hbn.) had been described, and even these had not been illustrated. When the genus was revised by Herrera and Field (1959) little more was known of its biology. *T. blanchardii* Butl. and *T. mercedis* (Esch.), common Chilean species, were reared but not published; *T. sterodice arctodice* Stgr. was studied as a truck-garden pest in an unpublished Colombian dissertation (Alvarez and Delgado 1969; Bravo *pers. comm.*). *T. autodice* has been redescribed several times, always unfigured, most recently by Margheritis and Rizzo (1965).

Recent studies (Shapiro 1978a, b and unpublished) indicate that the Andean Pierines are an important group for interpreting the historical biogeography and evolution of the regional biota. It thus becomes imperative to augment our knowledge of their biology. The descriptions which follow are based on field work in northern and central Argentina in 1977 and in southern Argentina in 1979 by the author, and in Chile in 1978 by Mr. C. V. Kellner. Alcoholic material will be deposited in the U.S. National Museum, Washington, D.C. and the University of California, Davis collections. Rearing was on continuous illumination at 25°C. Color descriptions in parentheses refer to the system of Kornerup and Wanscher (1978).

The *T. autodice* Species-Group

As defined by Herrera and Field this group contains two species and one subspecies. The adult characters make it a natural and very distinct group within the genus. Both species occur at low to moderate elevations.

*Tatochila autodice* (Hübner) (Fig. 1)

This is the common vacant-lot *mariposa blanca* of low elevations in northern and central Argentina. It colonizes in summer above 2000 m but does not seem to overwinter there. It is an occasional truck-garden pest, the *gusano rayado de las crucíferas* of Margheritis and Rizzo (1965). It was studied afield in the provinces of Tucumán, Córdoba, La Rioja, and Buenos Aires and in the Capital Federal (city of Buenos Aires) (26°49'S to 38°44'S). No geographic differences in morphology or development were observed.

Ecologically, *T. autodice* is largely confined to highly disturbed situations within regions supporting desert, subtropical forest, and temperate subhumid to subarid grassland biomes from at least 17°S to 40°S. Its occurrence in the desert is limited to river bottoms and washes. It is only an occasional stray in the humid Andes in Río Negro and Neuquén and does not normally breed at Bariloche. It is multivoltine throughout its range, with 5–6 broods in the northwestern provinces, about 4 at Buenos Aires, and perhaps 3–4 at Bahía Blanca. Winter is spent as a diapausing pupa. Diapause induction is under photoperiod-temperature control.

Eggs or larvae have been collected from the following wild crucifers in various locations: *Rapistrum rugosum* (L.), *Coronopus didymus* (L.) Smith, *Cardaria draba* (L.) Desv., *Cardamine hirsuta* L., *Diplotaxis muralis* (L.) DC., *Raphanus sativus* L., *Brassica geniculata* (Desf.) Ball (the most important host in Córdoba), *B. campestris* L., *B. napus* L., *Sisymbrium officinale* (L.) Scop., *S. irio* L., *Eruca sativa* Hill, *Coulingia orientalis* (L.) Dumort, and *Nasturtium officinale* R. Br. (all introduced from the Palearctic Region); and *Lepidium spicatum* Desv., *L. bonariense* L., *L. aletes* Macb., *Descurainia appendiculata* (Griseb.) Schulz and *D. argentina* Schulz (all native but weedy). Giacomelli (1915), citing Berg and Burmeister, recorded *T. autodice* on the genera *Cestrum* (Solanaceae) and *Medicago* (Leguminosae). Neither has been confirmed, and captive larvae rejected *Medicago sativa* L. and *M. hispida* Gaertn. Adults are common in alfalfa fields and often visit the flowers in the company of the alfalfa pest *Colias lesbia* (F.) and of *Tatochila vanvolxemii* (Capr.). Captive larvae do accept garden nasturtium, *Tropaeolum majus* L., and almost certainly use this indigenous genus (Tropaeolaceae) afield.

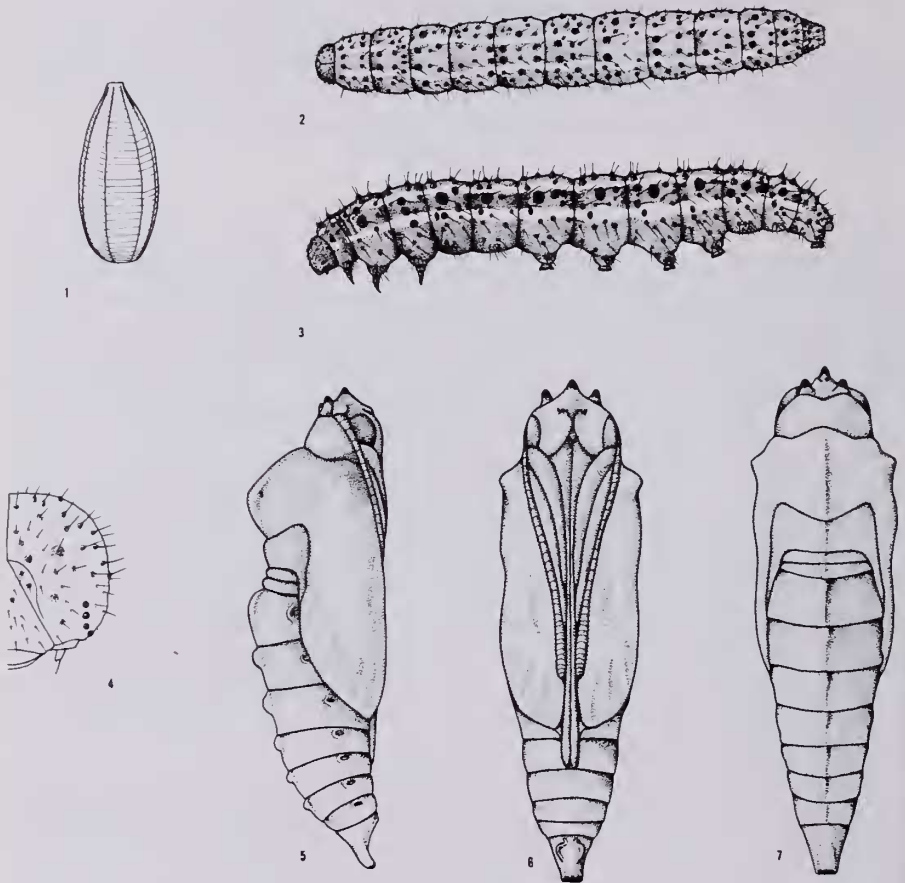


Fig. 1. *Tatochila autodice* from central Argentina: 1, egg; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, mature larva, head capsule; 5, pupa, lateral view; 6, pupa, ventral view; 7, pupa, dorsal view.

### Descriptions

*Egg*.—Erect, milk-bottle shaped,  $1.20 \times 0.35$  mm, the chorion sculptured as figured, with 8–10 vertical and about 32 horizontal ribs. Laid singly on leaves, stems, or inflorescences; when on leaves about equally on upper or lower surface. Often laid on small rosettes or on isolated plants along walls, hedgerows, or roadsides. Light orange when laid, darkening to deep orange after 12–18 h, translucent blackish 12 h before hatching. Time to hatch, 3–4 days. The larvae eat more or less of the chorion.

*Larva: first instar.*—At hatch 1.6 mm long at rest. Dull yellow with a black head, becoming grayish-green with full pattern (see below) of longitudinal pale yellow stripes after feeding. Numerous black tubercles bearing pale hairs. Begins by excavating pits in buds, flowers, green fruit, or leaves. Length of instar, 2 days.

*Second instar.*—After molt 5 mm. Slate gray with yellow stripes as follows: a faint mid-dorsal line; stronger subdorsal; and stigmatal. Head slate gray. Ocelli and true legs black; venter and prolegs greenish-gray. Head and body with many black tubercles falling into 3 size classes, surmounted by whitish hairs. Length of instar, 2–3 days.

*Third instar.*—After molt 9.4 mm. Similar, the yellow dorsal line tending to disappear; feeds openly near top of plant on inflorescences and leaves. 3–4 days.

*Fourth instar.*—After molt 15.3 mm. As before, the mid-dorsal line often completely lost. 3–4 days.

*Fifth instar.*—After molt 25.4 mm, when full grown 34 mm. Head gray with many black tubercles, each bearing a whitish hair, and faintly mottled in orange. Body with the yellow dorsal line barely if at all visible within a broad dorsal stripe of gray (“grayish turquoise,” 24E3); below this are greenish-yellow (“primrose yellow,” 1A6) subdorsal stripes including two orange (6A6) dots and two large black tubercles on each segment; below this a gray (24E3) stripe and below it a yellow (1A6) stigmatal stripe containing two orange (6A6) dots, one anterior and one posterior to the spiracle; shading into blue-green (“greyish green,” 25D5) which continues across the venter, including the prolegs. Body with numerous black tubercles as shown, some conical, each bearing a short whitish hair. The anterior ends of all of the yellow stripes on the prothorax are orange and expand to form a narrow orange “collar” directly behind the head.

Occasional aberrant larvae have been found in which the dark stripes are dark bluish green (“opaline green,” 25C6) or else purplish gray (“dull violet,” 16D3) with the light markings all orange (6A6). The former seems to be genetically determined, while the latter is associated with parasitism by the Braconid *Apanteles ayerzai* Brethes.

Mature larvae “stem” the hosts and sit on the bare stalk, where the striped pattern is highly cryptic. The final one or two fecal pellets are red. Length of instar, 6–7 days.

*Prepupa.*—Vertical, head up, attached in usual Pierid fashion by the anal prolegs and a silken girdle around the thorax. The color does not change conspicuously (unlike the genus *Euchloe* of the Holarctic, with a similar larva). Unlike most Pierines, the mature larva does not wander before pupation and usually attaches itself to the host, either on the bare stem or (if the host is quite leafy) on the underside of a leaf. 18–30 hours.

*Pupa.*—Length 24–25.5 mm, the female noticeably larger. Width at girdle

5–5.5 mm. Initially colored like the larva, assuming its final coloration in 4–6 h. Ground light pinkish gray ("pinkish white," 9A2) with numerous but inconspicuous black tubercles corresponding to those of the larva; dorsal midline strongly carinate on the thorax, with a series of black-tipped smaller keels anteriorly on the abdominal segments; frontal and supraocular prominences all the same size, black, 3 dorsolateral flaring prominences above the spiracles moderately developed, not marked with black; two rows of light orange dots, each with two to a segment, on either side of the dorsal midline and in line with the spiracles, corresponding to their larval positions although the yellow stripes containing them are essentially lost; eyes and appendage cases, including wings, light gray (7B1), unmarked except for a black spot at the end of the discal cell and tiny black dots along the outer wing margin. Spiracles black. Cremaster light gray. Thorax mottled dorsally with olivaceous gray ("brownish grey," 6C2); frons and vertex creamy white, contrasting. The color scheme of the pupa is invariant and reminiscent of *Pieris beckeri* Edwards of western North America. It is probably a bird-dropping mimic. The shape is more slender and angular than *T. xanthodice* Lucas (Shapiro 1978b).

Before eclosion the eyes, wings, and body are pigmented in that order. White is laid down 12–18 h before black. Meconium red. Length of instar 6–10 days.

#### *Tatochila blanchardii* Butler (Fig. 2)

*T. blanchardii* is the ecological equivalent of *autodice* in Chile, from Tarapacá (20°S) to Cautín (39°S) and crossing the Andes into the Argentine provinces of Chubut and Río Negro, including the Nahuel Huapí National Park and the Bariloche district, where *autodice* is a rare casual. In the Central Valley of Chile it is common in disturbed urban and agricultural habitats and breeds on the introduced Crucifers *Rapistrum rugosum*, *Sisymbrium officinale*, and *S. orientale* L. Herrera and Field (1959) and Peña (1975) suggest Tropaeolaceae as hosts, perhaps following Giacomelli (1915). *Tropaeolum majus* is accepted by the larvae.

The species is multivoltine, with about four generations per year at Santiago (September–May). At Bariloche, where it breeds on *Brassica geniculata* and *Sisymbrium officinale*, it has at least two generations with perhaps a partial third. Winter is spent as a diapausing pupa.

The following descriptions are based on a composite of material from the Chilean Central Valley (*leg.* Kellner) and bred *ex ovo* from Bariloche.

#### Descriptions

*Egg*.—Similar to *T. autodice*, slightly smaller,  $1.10 \times 0.30$  mm, with 8–9 vertical and about 32 horizontal ribs. Laid singly on stems, fruits, flowers,

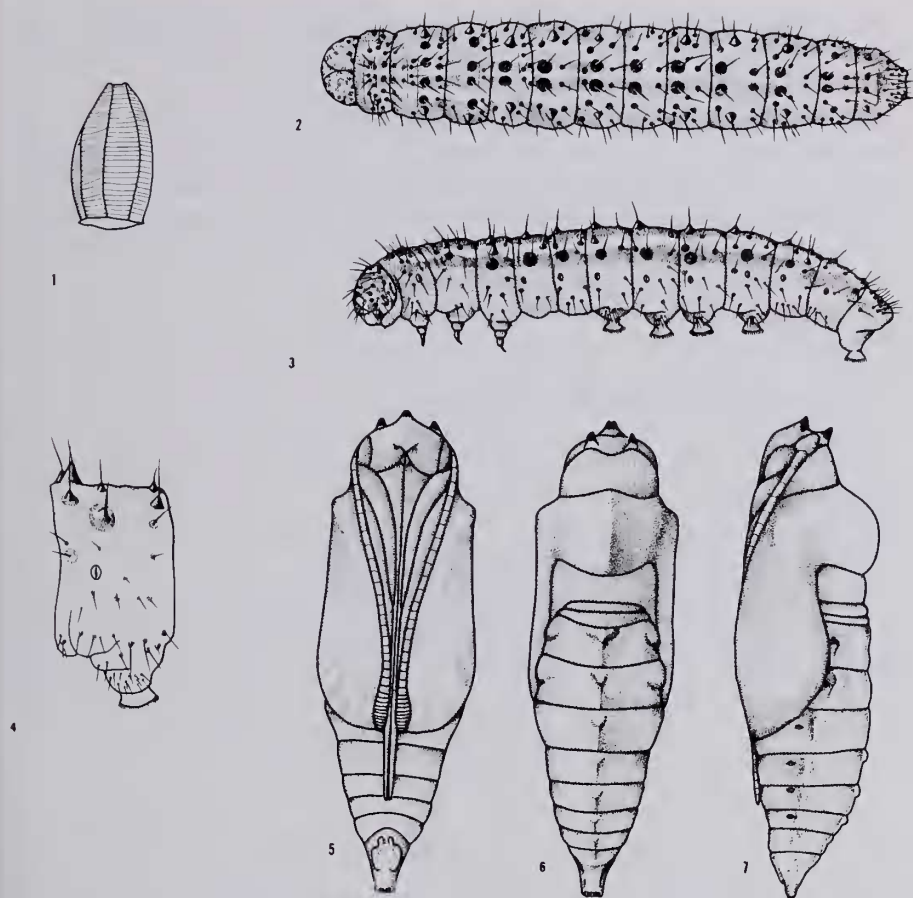


Fig. 2. *Tatochila blanchardii* from Santiago, Chile: 1, egg; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, lateral view of seventh segment, showing major tubercles; 5, pupa, ventral view; 6, pupa, dorsal view; 7, pupa, lateral view.

and indiscriminately on upper and lower surfaces of leaves. Usually laid on plants in at least partial shade. Light orange when laid, darkening to deep orange after 12–18 h, and to translucent blackish 12 h before hatch. 3 days.

*Larva: first instar.*—At hatch 1.5 mm at rest. Yellow, with black head; becoming dark gray-green with full *Tatochila* pattern after feeding. Length of instar, 2–3 days.

*Second instar.*—After molt 4.5 mm. Black, with a barely discernible yellow mid-dorsal line; two strong subdorsal yellow stripes; shading into gray from the spiracles across the venter, including the prolegs. Head dark gray, ocelli black. Tubercles as in *autodice* but more prominent, bearing whitish hairs; the largest with dark hairs. Length of instar, 3 days.

*Third instar*.—After molt 7 mm. Similar; resting for long periods on the stem, where highly cryptic. Length of instar, 3 days.

*Fourth instar*.—After molt 12.0 mm. As before. 3–4 days.

*Fifth instar*.—After molt 19 mm, reaching 29.5 mm when full-fed. The most slender *Tatochila* larva yet reared. Mustard yellow (2A6) with very prominent large tubercles as shown, bearing dark hairs; smaller tubercles in two sizes, less conical, bearing light hairs. With a narrow but well-defined mid-dorsal yellow line and subdorsal stripes, about three times as wide and of the same color (2A6); dark stripes purplish-gray (13D2), containing a row of very large tubercles directly above the spiracles; pleural and ventral areas light grayish yellow, the venter slightly green-tinged, separated by a diffuse purplish-gray line. Spiracles black. Head gray with irregular yellowish mottling and many black tubercles; ocelli black.

As in *T. autodice*, the larva eats all parts of the plant, "stemming" it. It rests low on the bare stem. The final one or two fecal pellets are red. Length of instar, 3–5 days.

*Prepupa*.—Vertical, head up, as in *T. autodice*; at Bariloche commonly on the host. Length of prepupal period 18–30 h.

*Pupa*.—Length 21 mm, width at girdle 6 mm (reared *T. b. ernestae* Herrera, from extreme northern Chile, average only 19 × 4.9 mm but do not differ in color and pattern). Similar to *T. autodice* in color and pattern, but slightly stockier; with broad olivaceous gray (6C2) stripes above the spiracles, dorsad of the flaring prominences, concolorous with the dorsal thoracic mottling. Meconium red. Length of instar, 7–12 days.

### The *T. sterodice* Species-Group

This is a very homogeneous group of six named entities: *T. sterodice* with four subspecies, *T. vanvolxemii*, and *T. mercedis*. All of these are apparently allopatric (or in the case of *T. s. macrodice* and *T. vanvolxemii*, isolated by altitude). *T. sterodice* has the widest latitudinal range of any South American butterfly, from central Colombia (3°N) to Tierra del Fuego (55°S). The other species are confined to the temperate mid-latitudes.

All lay orange eggs, which differ among themselves in the sculpturing of the chorion; all are more fusiform than in the *autodice* group. All have stocky larvae and pupae, relative to that group. The larvae are striped lengthwise in black and yellow, generally with complete *Tatochila* pattern (yellow mid-dorsal line, subdorsal stripes and a broken stigmatal line which may be reduced to pairs of spots, one anterior to and one posterior to, each spiracle). When mature they are somewhat lighter in ground color and have a pronounced resemblance to some Noctuid "cutworm" larvae, from which they differ in having many black tubercles in three sizes, bearing light hairs. The pupae are smooth, without the abdominal keels and with only rudi-

mentary dorsolateral prominences, and resemble the pupa of *T. xanthodice* except for the much longer proboscis case in this group.

All the species are associated with weedy Crucifers in highly disturbed habitats, and are today mainly anthropophilic. No member of this species-group has been recorded on Tropaeolaceae to date. All known populations, except perhaps *T. s. fueguensis* from Tierra del Fuego, are at least bivoltine and overwinter as a pupa under photoperiod-temperature induced diapause (except *T. s. arctodice*, which breeds continuously).

#### *Tatochila sterodice* Staudinger

The four races of this Andean insect replace one another latitudinally and are associated with major physiographic-ecological regions: *T. s. arctodice* in the northern Andean *altiplano*, *T. s. macrodice* in the *puna*, *T. s. sterodice* in the Patagonian Andes, and *T. s. fueguensis* in the subantarctic forest region. The last two are probably clinal across southern Patagonia and the Isla Grande de Tierra del Fuego. The most distinct of the subspecies is *arctodice* Stgr., which is circumequatorial and uniquely in the group does not appear to diapause. Its biology was studied by Alvarez and Delgado (1969) and will not be repeated here. The other three subspecies all occur in Argentina; their early stages show no more differentiation than the adults.

#### *Tatochila sterodice macrodice* Staudinger (Fig. 3)

This subspecies was studied around Tañi del Valle, Province of Tucumán, in a dry-montane environment in one of the isolated ranges east of the Andes proper (27°S). It was found in vacant lot and roadside habitats, exploiting weeds such as *Descurainia argentina*, *Brassica geniculata*, and *Lepidium* sp. (? *ruderales* L.). In Salta and Jujuy it occurs above 3000 m (B. MacPherson, R. Eisele, *pers. comm.*) and perhaps has native non-weedy hosts. The range extends to southern Peru, extreme northern Chile, east into Bolivia and south in Argentina to Mendoza, where it may intergrade to the next. All records known to me are from above 1500 m.

Males are vigorous "hilltoppers." The behavior of this subspecies was described in detail by Jörgensen (1916). In northwestern Argentina its flight season is November to April, with two or three broods.

#### Descriptions

*Egg*.—Erect, fusiform,  $1.15 \times 0.40$  mm, with about 16 vertical and 35 horizontal ribs. Bright orange when laid, scarcely darkening until 12 h before hatch when it becomes translucent blackish. Time to hatch, 5–6 days. The eggs are laid singly on stems, inflorescences, and cauline leaves of larger



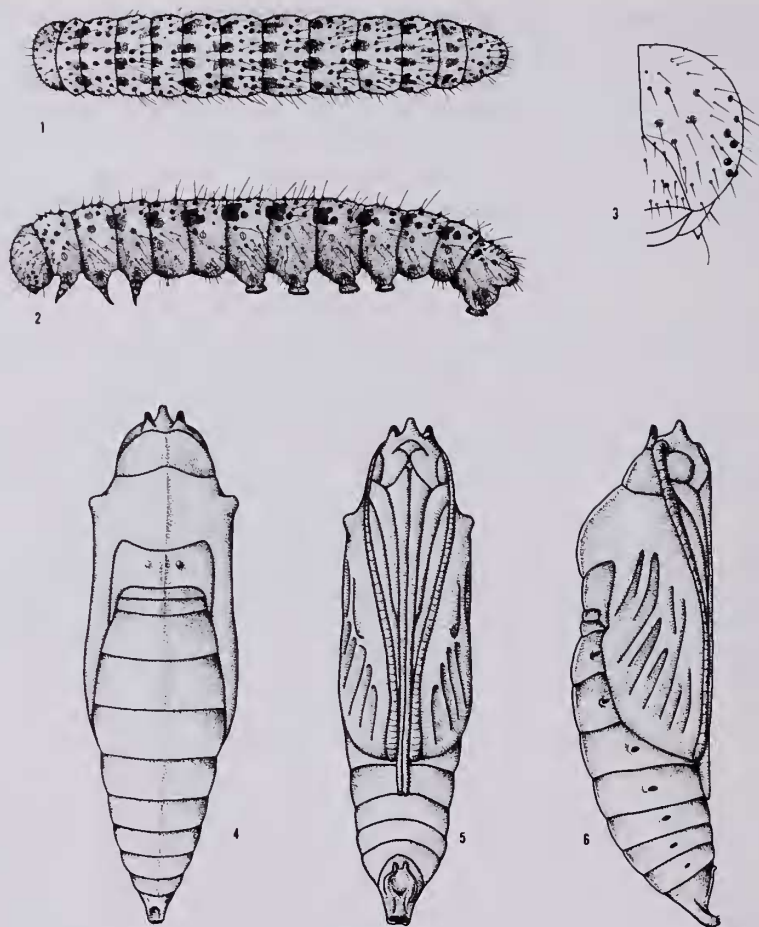


Fig. 3. *Tatochila steroidice macrodice* from Tafí, Tucumán, Argentina: 1, fifth instar larva, dorsal view; 2, fifth instar larva, lateral view; 3, mature larva, head capsule; 4, pupa, dorsal view; 5, pupa, ventral view; 6, pupa, lateral view.

plants, and also on the upper surfaces of small rosettes. More than half the eggs seen at Tafí were laid on apical buds.

*Larva: first instar.*—At hatch 1.4 mm. Pale yellow with dark brown head. After feeding olive green with the usual yellow pattern at first weakly, then more strongly indicated, with many black tubercles. The larva eats pits in soft tissue, preferably of buds. It eats its entire chorion. Time to molt, 2 days.

*Second instar.*—After molt 4 mm. Black, with lemon yellow stripes in the

full *Tatochila* pattern; tubercles, ocelli and spiracles black; venter gray. Length of instar, 2–3 days.

*Third instar*.—After molt 6.5 mm. Same pattern, with indistinct orange spots at the anterior end of each subdorsal yellow stripe on each segment, and on either side of each spiracle. Mid-dorsal yellow line strong. When not feeding the larva sits along the stem. 3 days.

*Fourth instar*.—Length after molt 10.5 mm. Subdorsal stripes less bold, the mid-dorsal one persistent. Length of instar, 4 days.

*Fifth instar*.—After molt 18.5 mm, reaching 30–32 mm at maturity. Body blackish gray ("medium grey," 1E1); mid-dorsal yellow line distinct, the subdorsal stripes less so but containing an orange spot at the anterior, and sometimes the posterior, end on each segment; a distinct orange spot anterior, and a less distinct one posterior to each spiracle; venter dull gray ("pastel grey," 1C1). Tubercles in 3 size classes, black, bearing light hairs. The stripes of ground color contain large squarish black spots anteriorly as figured, on the dorsum of each segment; they occur throughout the species-group. Larvae "stem" the host, sitting low on the leafless stalk, usually head down. The last fecal pellets are red. Length of instar, 6 days.

*Prepupa*.—Formed at some distance from the host, the larva wandering without feeding for 2–6 h. Time to molt, 14–27 h.

*Pupa*.—22.5 × 5.5 mm. Initially deep slate-green ("greyish green," 25D5); within 8 h turning light pearly gray ("reddish grey," 9B2); with numerous small black tubercles corresponding to their larval positions, but inconspicuous; dorsal and subdorsal lines as in the larva, whitish, the latter containing faint orange dots anteriorly on each segment; the orange amphspiracular spots also faintly indicated on the abdomen. Head and appendages—including wing-cases—ochreous ("greyish yellow," 4B4) with variable but rarely extensive black filling between veins on the outer half, and a black discocellular dot. Attached vertically, head up, on dry weeds, fence-posts, walls, etc. Pigment sequence as usual; meconium red; time to hatch, 8–13 days.

Some pupae of *T. s. macrodice* have a series of black dots anteriorly on the dorsal abdominal midline, corresponding to those in the *autodice* group.

#### *Tatochila sterodice sterodice* Staudinger (Fig. 4)

Cultures were established from localities near the northern and southern extremities of the range of this subspecies: San Carlos de Bariloche, Río Negro (41°08'S) and Río Gallegos, Santa Cruz (51°37'S), the latter transitional to *T. s. fueguensis* Field. No morphological differences were noted, but Río Gallegos stock grows more rapidly, its mean time from oviposition to eclosion being 3–4 days shorter. Data given below are for Bariloche, where the population is partially triple-brooded (October to March). At Río

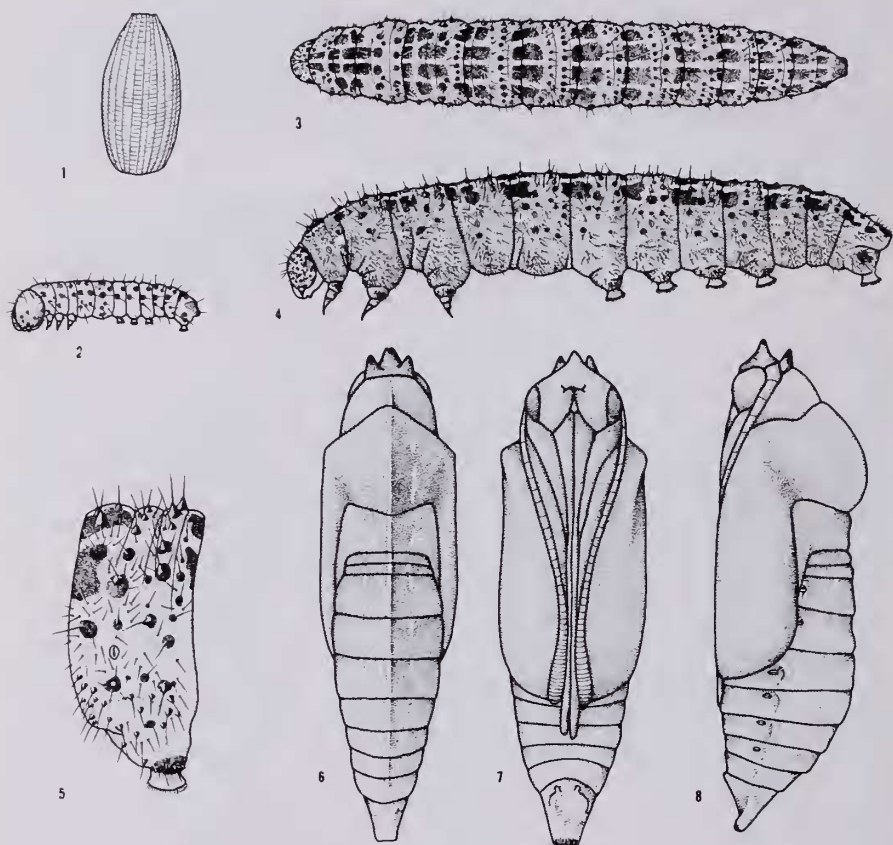


Fig. 4. *Tatoschila sterodice sterodice* from Bariloche, Argentina: 1, egg; 2, newly hatched larva showing primary tubercles and setae; 3, mature larva, dorsal view; 4, mature larva, lateral view; 5, lateral view of seventh segment, showing major tubercles; 6, pupa, dorsal view; 7, pupa, ventral view; 8, pupa, lateral view.

Gallegos it is probably at least partially double-brooded (November–February). Winter is spent as a diapausing pupa. Although males “hilltop,” this subspecies is often found in areas of uniform low relief.

The recorded hosts are numerous and all of Palaearctic origin: at Bariloche: *Rapistrum rugosum*, *Coronopus didymus*, *Lepidium ruderales*, *L. perfoliatum*, *Raphanus sativus*, *Brassica geniculata*, *B. campestris*, *Sisymbrium officinale*, and *S. irio*. At Río Gallegos: *Cardaria draba*, *L. perfoliatum*, *R. sativus*, *B. geniculata*, *B. campestris*, *B. kabera* (DC.) Wheeler, *S. officinale*, *S. altissimum* L., and *S. irio*. There are no native Crucifers on the Patagonian coast, where *sterodice* is common in all the larger towns.

## Descriptions

*Egg*.—As in the preceding,  $1.12 \times 0.37$  mm, with about 18 vertical and 35 horizontal ribs, dull orange when laid, darkening slightly after 6–12 h, becoming blackish-translucent 8–12 h before hatch. Laid singly on buds and stems of flowering plants and commonly on leaves of rosettes. Time to hatch, 6 days.

*Larva: first instar*.—At hatch 1.4 mm long. Pale yellow with brown head; after feeding olive green with the full yellow *Tatochila* pattern. Tubercles black. On flowering plants the larva consumes the buds; on rosettes it excavates pits. Time to molt, 4 days.

*Second instar*.—Length after molt, 3.9 mm. Olive green, the usual pattern yellow, with strong mid-dorsal and subdorsal lines and numerous black tubercles. Feeds by preference on flowers and young, green fruit. 3 days.

*Third instar*.—After molt 7.2 mm. Blackish olive ("greyish green," 28E5) with the full yellow pattern, including distinct amphispircular spots. 4–4.5 days.

*Fourth instar*.—After molt 10.5 mm. As before, the dark blotches on the anterior portion of each dorsum more conspicuous; orange spots at the anterior end of each subdorsal stripe on each segment, and on both sides of the spiracles. Time to molt, 5 days.

*Fifth instar*.—After molt 17 mm, reaching 28 mm. Olivaceous gray-green ("olive," 3E6) with a well-defined mid-dorsal and pair of subdorsal lines, all of about equal width, yellow; an orange dot within each subdorsal line at the anterior end of each segment; orange dots anterior and posterior to each spiracle (in about 40% of larvae these dots are yellow); subspiracular area and venter, including prolegs, greenish gray (1D2); head brownish-gray mottled with orange, tubercles and ocelli black. Body with many tubercles falling in three size classes, surmounted by fine pale hairs.

The larva "stems" the plant and as usual sits lengthwise on the stem, head up or down. Last fecal pellets red. Time to molt, 7–8 days.

*Prepupa*.—Wandering for 3–8 h before spinning. Vertical, head up. 18–36 h.

*Pupa*.—Length 20.5–22 mm, width at girdle 5–6 mm. Initially slate green ("greyish green," 25D7), assuming its final coloration in 6 h. Colored exactly as in *T. s. macrodice*, generally with little black filling on the wing-cases. Dorsolateral prominences very weak. Frontal and supraocular prominences equal, black. Pre-hatch pigmentation sequence normal, meconium red. 8–15 days. This is the slowest-developing *Tatochila* yet reared.

*Tatochila vanvolxemii* (Capronnier) (Fig. 5)

Distributed in Argentina from the Province of Tucumán (27°S) to Río Negro and southern Buenos Aires (40°S) in subhumid to subarid grassland,

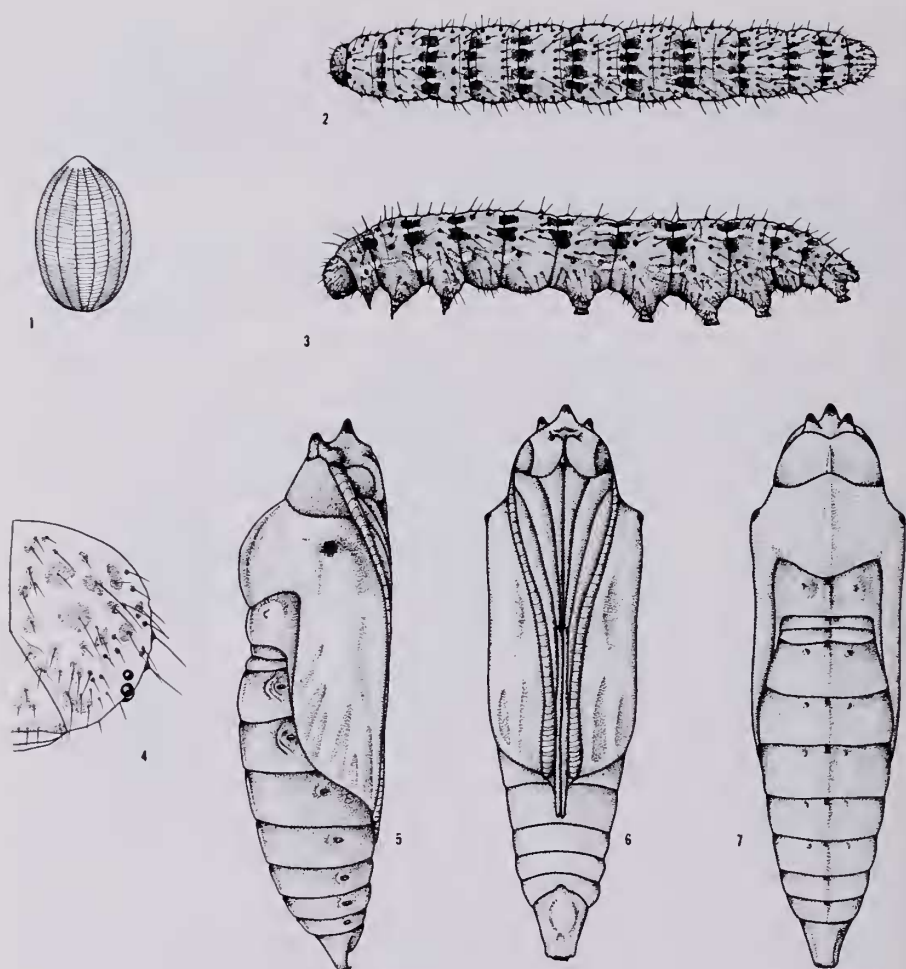


Fig. 5. *Tatochila vanvolxemii* from central Argentina: 1, egg; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, mature larva, head capsule; 5, pupa, lateral view; 6, pupa, ventral view; 7, pupa, dorsal view.

its ecological range almost exactly matching that of the North American *Pieris protodice* Bdv. & LeC. which it also resembles phenotypically. It is very abundant in disturbed sites and has been recorded on both native and introduced Cruciferous weeds: *Rapistrum rugosum*, *Coronopus didymus*, *Cardaria draba*, *Lepidium* (several species), *Descurainia appendiculata*, *Raphanus sativus*, *Brassica geniculata*, *Sisymbrium officinale*, *S. altissimum*, and *Eruca sativa*. Of these *B. geniculata* and the *Lepidium*s seem to be most often used. The species is 3-5-brooded in various parts of its range,

overwintering as a pupa in photoperiod-and-temperature-induced diapause. Jörgensen (1916) records it from early October to mid-May in Mendoza at 937 m. Primarily a lowland species, it does not appear to "hilltop."

Stocks were obtained from Córdoba and Capilla del Monte, Province of Córdoba (31°S) and Bahía Blanca, Province of Buenos Aires (38°44'S), near its northern and southern range extremities. No morphological or developmental differences were found. Both stocks are polymorphic for a number of adult and larval characters.

### Descriptions

*Egg*.—Usual form,  $1.2 \times 0.33$  mm, when laid light yellow to yellowish-orange, usually but not always darkening to deeper orange after 6 h (the difference appears to be hereditary through the female line); with 12–15 vertical and 34–37 horizontal ribs. Becomes opaque and hyaline 12 h before hatch. Laid singly on buds, fruit, stems or leaves. This species produces very large numbers of eggs per female, sometimes over 600 (Margheritis and Rizzo, 1965 quote a figure of 4–500 for *T. autodice*). Time to hatch, 3–4 days.

*Larva: first instar*.—At hatch 1.6 mm. Dull olivaceous-yellow, head black. Feeds preferentially on flowers, but will eat pits in leaves; becoming gray-green with full yellow pattern. 2 days.

*Second instar*.—3.3 mm after molt. Slate gray, with full yellow pattern and numerous black tubercles. Time to molt, 2–3 days.

*Third instar*.—Length after molt 9.5 mm. Slate gray with the usual yellow pattern of a mid-dorsal line and subdorsal lines, about twice as broad; a yellow spot anterior and posterior to each spiracle, the size and shape of these spots variable; four blackish blotches on the anterior dorsum on each segment, as illustrated; head gray, mottled with dull yellow, ocelli and tubercles black. Venter and prolegs gray. True legs and tubercles black, the latter in three size classes, bearing light hairs. Feeds on all parts of the plant. 3–4 days.

*Fourth instar*.—15.5 mm. Head gray, with a yellow cast. Yellow amphispiracular spots frequently connected to form a zigzag stripe. Faint orange spots occasionally present anteriorly in the subdorsal lines on each segment. The mid-dorsal line weak but still present. 3–4 days.

*Fifth instar*.—After molt 25 mm, reaching 33.5 mm. As before, the ground color becoming dingy mouse-brown ("greyish brown," 5D3), producing a very cutworm-like effect, with the black dorsal blotches strongly contrasting; the spiracular spots joined in a line in about 65% of the larvae, otherwise variously shaped, sometimes partly or all orange. As usual the larvae "stem" the host and sit on the bare stalk. The last fecal pellet or two are red. Time to molt, 5–7 days.

*Prepupa*.—Attached in the usual manner, vertical, head up, after a wandering period of 4–6 h or more. Duration of prepupal period, 12–20 h.

*Pupa*.—21.5 × 5.6 mm. At first slate green ("greyish green," 25D7), within 6 h colored exactly as in *T. s. macrodice*; black filling on wing cases variable, rarely pronounced. Black dots on dorsal abdominal midline almost always present and conspicuous. Dorsolateral prominences very weak. Frontal and supraocular prominences equal, black. Eyes, wings and body become pigmented in that order; white is laid down 30 h, black 12 h, before eclosion, which is almost always within 30 min of sunrise. Meconium red. Length of instar 6–9 days.

Wild pupae occur on walls, fence posts, rubbish, and dry weeds and have not been found on the host. If *T. vanvolxemii* breeds on any of the Capridaceous shrubs which occur in its range it might pupate on them.

#### *Tatochila mercedis* (Eschholtz) (Fig 6)

This small species is the most aberrant in the group. It occurs in Mediterranean Chile from Atacama to Llanquihue (27°–41°S), generally in highly disturbed habitats in agricultural or waste ground on valley floors and in foothill canyon bottoms. It is multiple-brooded (August–April at Santiago; five broods?) and winters as a diapausing pupa. Its recorded hosts are *Rapistrum rugosum*, *Raphanus sativus*, *Brassica campestris*, *Sisymbrium officinale* and *S. orientale*. All of these are European, and Peña (1975) predicts that a native Chilean host will be found.

*T. mercedis* is occasionally recorded at Bariloche, Argentina (Herrera and Field 1959) and—obviously in error—in subtropical Misiones, north-east Argentina, by Breyer (1938). Giacomelli (1915) recorded it also from Bolivia, but there are no recent records from there.

#### Descriptions

*Egg*.—Similar to the others in this species-group but slightly smaller, 1.05 × 0.27 mm, with about 16 vertical and 33 horizontal ribs. Dull orange when laid, deepening in color after about 6 h; translucent blackish 12 h before hatch. Laid singly, mostly in inflorescences, but also on leaves of small rosettes. Time to hatch, 3–4 days.

*Larva: first instar*.—Dull yellow with black head; 1.05 mm at hatch. Feeds preferentially on buds, flowers or young fruit, but will excavate pits in leaves. Becoming gray-green with the usual yellow pattern after feeding; time to molt 2 days.

*Second instar*.—After molt 2.3 mm. Black, with the following yellow markings: a weak mid-dorsal line; a stronger, wider subdorsal stripe on each side; spots anterior and posterior to the spiracles. Head dark gray. Venter and prolegs dull greenish gray. Tubercles, prolegs and ocelli black. Length of instar, 3 days. (The spiracular spots may be orange.)

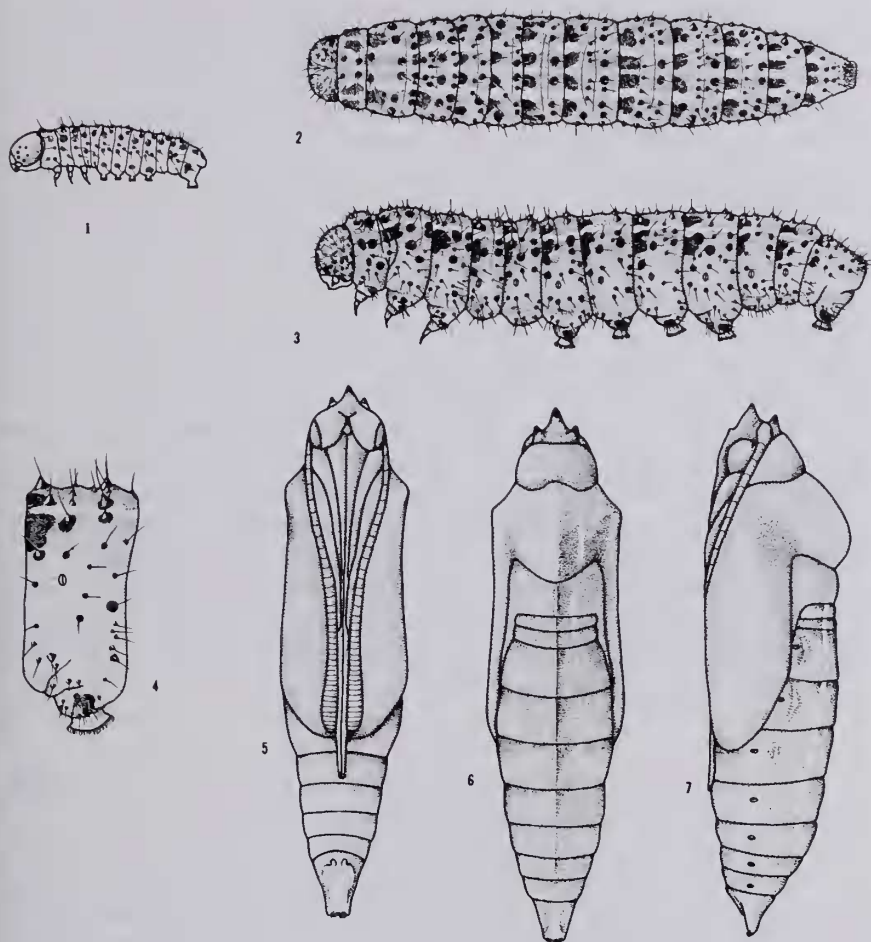


Fig. 6. *Tatochila mercedis* from central Chile: 1, newly hatched larva showing primary tubercles and setae; 2, mature larva, dorsal view; 3, mature larva, lateral view; 4, lateral view of seventh segment, showing major tubercles; 5, pupa, ventral view; 6, pupa, dorsal view; 7, pupa, lateral view.

*Third instar.*—After molt 4.2 mm. Pattern as before. Feeds in the open on the upper portion of the plant. Length of instar, 3–4 days.

*Fourth instar.*—Length 8.2 mm. Pattern as before, the dark blotches on the anterior dorsum of each segment becoming distinct. Tubercles conspicuous, black. 2–3 days.

*Fifth instar.*—15.5 mm, reaching 23 mm. Somewhat lighter, body gray-black ("medium grey," 1E1) with distinct black dorsal blotches as shown; usual pattern primrose yellow (1A6), the amphispiracular spots variable, sometimes connected in a zigzag line as in *T. vanvolxemii*, the dorsal midline



still visible but narrow. Venter dull gray ("pastel grey", 1C1). Head brownish-gray with a yellow cast. Tubercles, ocelli, and true legs black. The large tubercles are more conical in this species than in the others of the group, suggesting *T. blanchardii*.

Habits as in the other species, "stemming" the plant. Last fecal pellets red. Time to the prepupa, 6 days.

This description applies to larvae reared on slender Crucifers. When reared on heart leaves of cabbage (*Brassica oleracea* L.) lighter in color: ground brownish gray (7D3), the yellow markings paler and more extensive, making the tuberculation more contrasting.

*Prepupa*.—Head up, attached in the usual manner. Length of prepupal period, 14–20 h. Captive larvae wander for 3–6 h before spinning.

*Pupa*.—20 × 4.5 mm. Distinctively slender, but the dorsolateral prominences still weak. Frontal prominence often less blackened than the supraoculars, but of similar size. At first slate green ("greyish green," 25D7), but within 6 h turning buffy gray ("greyish orange," 5B3); wing-cases scarcely contrasting but sometimes slightly ochreous, without black filling between the veins; dorsal and subdorsal yellow lines preserved, along with numerous but inconspicuous black tubercles; spiracles black; a few black points along veins and wing margins, but little or no dark discal spot. Eyes, wings, and body pigmented in that order, white appearing 20 h, black 8–12 h, before eclosion. Meconium red. Length of instar, 8–11 days.

### Discussion

Both species-groups recognized by Herrera and Field (1959) on adult characters are cohesive in their immature stages, as well.

The larval coloration of *Tatochila* seems very conservative. Within the *sterodice* group the differences among species are scarcely greater than those between subspecies. The most distinctive member of the group is *mercedis*, and its characters seem to bear on the evolutionary affinities between the *autodice* and *sterodice* groups.

Giacomelli (1915) derived the entire genus from *autodice*, making "*theodice*" (actually *blanchardii*) a very early offshoot, "*volxemi*" (*vanvolxemii*) next, then the *sterodice* group, even while admitting that "one must say in truth that *volxemi* is of doubtful placement and, more than all the other *Tatochila*, is of uncertain affinities." Giacomelli did not know the genitalic characters used by Herrera and Field (1959) in placing *vanvolxemii* solidly into the *sterodice* group (they found that the male genitalia of *sterodice* and *vanvolxemii* were indistinguishable). The early stages unambiguously support this judgment and at the same time suggest that the member of the group closest to *autodice* and *blanchardii* is not *vanvolxemii* but *mercedis*.

The dorsal pattern of both sexes of *autodice* and of the male *blanchardii* is a reduction of the full *Tatochila* pattern (still expressed in female *blan-*

*chardii*, and in males of ssp. *ernestae*). Of the other *Tatochila*, *mercedis* and some individual *sterodice* show the closest approximation to *autodice* dorsally. On the ventral hindwing, *autodice* and *blanchardii* almost always have an isolated spot in interspace Sc + R<sub>1</sub>. Elsewhere in the genus this spot appears frequently in *mercedis* and occasionally in *sterodice* and nowhere else. In both it is usually connected to the vein. It represents pigment deposition in an aborted vein trace and may imply a phylogenetic connection between the *autodice* group and *mercedis-sterodice*. (This must be interpreted with caution; the same spot appears, obviously independently, in some stocks of Nearctic *Pieris napi* (L.)!) This hint is borne out in the larvae and pupae of *mercedis*—in the prominence of conical subdorsal tubercles on the larva, suggestive of *blanchardii*, and in the slender pupal shape.

*T. mercedis* is confined to Chile, a fact which bears on the direction of evolution in these groups. Due to its isolation Chile has a depauperate butterfly fauna (Peña, 1975) mostly derived from the Andes. With *sterodice* so widely distributed in the Andes it would more likely be ancestral to *mercedis* than the reverse; if the *mercedis-autodice* group connection is real, the likelihood that the *sterodice* complex *in toto* is derived from the *autodice* group is very low. Thus evolution is more likely to have proceeded from the *sterodice* to the *autodice* group than the reverse (as postulated by Giacomelli). *T. s. arctodice* of the northern Andes is phenotypically very close to the sympatric *T. xanthodice*, which on genitalic grounds is grouped by Herrera and Field (1959) with *T. distincta* Jörg. in a separate species-group. The early stages of *xanthodice* and of the *sterodice* group are also very similar, differing primarily in the number of ribs in the egg and the length of the pupal proboscis-case. Tentatively these two species-groups may be considered close, and primitive relative to the *autodice* group.

Parallel and convergent adaptations occur repeatedly in the Holarctic and Andean Pierid faunas. The rounded, stocky pupae of the *sterodice* group are approached by the montane and alpine members of the Holarctic *Pieris* (*Synchlloe*) *callidice* Hbn. complex. The striped pattern is a very widespread one in the family, but there is an almost uncanny resemblance among the mature larvae of *Tatochila autodice*, *Pieris protodice*, and the Eulichloine *Euchloe ausonides* Lucas. The angular pupa of the *autodice* group is similar in shape to the Holarctic *Pieris rapae* (L.) and *P. napi* (L.) species-groups, but less extreme than the latter. In South America this trend is carried to its apex in *Ascia monuste* (L.), in which the dorsolateral prominences are prolonged into curving black spines. The angularity of the pupa in Pierini seems very broadly correlated with environmental humidity, but there are too many exceptions to make this a cause-and-effect argument. "Bird dropping mimicry" occurs in the pupae of *Pieris beckerii* Edw. in western North America, and in *A. monuste*, which like *T. autodice* often pupates on the host. In subsequent phenetic or cladistic analysis of Pierini, including life

history traits, it will be necessary to keep in mind that bewildering, non-concordant parallelisms occur again and again in Pierine evolution (as noted for adult characters by Field (1958).)

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Department of Zoology, University of California, Davis, California 95616.

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